

Does timing of breeding matter less where the grass is greener? Seasonal declines in breeding performance differ between regions in an endangered endemic raptor

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Abstract

The timing of breeding can strongly influence individual breeding performance and fitness. Seasonal declines in breeding parameters have been often documented in birds, particularly in the Northern Hemisphere. Fewer studies have investigated whether seasonal declines in productivity vary in space, which would have implications for a species' population dynamics across its distributional range. We report here on variation in the timing of breeding in the Black Harrier (*Circus maurus*), an endangered and endemic raptor to Southern Africa. We investigated how key breeding parameters (clutch size, nesting success and productivity) varied with the timing of breeding, weather conditions (rainfall and temperature) and between contrasted regions (coastal vs. interior-mountain). Black Harrier onset of breeding extended over an 8-month period, with a peak of laying between mid-August and end of September. We show a marked seasonal decline in all breeding parameters. Importantly, for clutch size and productivity these seasonal declines differed regionally, being more pronounced in interior-mountain than in coastal regions, where the breeding season was overall shorter. Timing of breeding, clutch size and productivity were also partly explained by weather conditions. In coastal regions, where environmental conditions, in particular rainfall, appear to be less variable, the timing of breeding matters less for breeding output than in interior-mountain regions, and breeding attempts thus occurred over a longer period. The former areas may act as

population sources and be key in protecting the long-term population viability of this threatened endemic raptor. This study provides unique evidence for a regionally variable seasonal decline in breeding performance with implications for population biology and conservation.

Keywords

Black Harrier, *Circus maurus*, Conservation, Breeding success, Productivity, Fynbos, Karoo, South Africa

Introduction

Understanding spatial-temporal variations in breeding parameters is an essential component of population ecology, and is particularly important for species that are of conservation concern, as this may help identify reasons for population decline or scarcity (Newton 1979, 1998, Krebs 1985). In this context, understanding variation in the timing of breeding and its potential fitness consequences is an essential intermediate step, and may reveal limiting factors for the species (Perrins 1970, Verhulst 2008). Quality of the breeding area, predation risk, inter- and intra-specific competition, individual quality and time of migration (Newton 1998) have all been found to affect timing of breeding in bird species. Overall, weather conditions (Charmantier et al. 2008, Visser et al. 2009) and food abundance (Newton 1998, Verboven et al. 2001) are generally considered the two main drivers influencing variation in the timing of breeding in bird species. In tropical birds, breeding onset may occur throughout the year as a result of a less seasonal climate and more constant food availability and abundance (Simmons 2000, De Marchi et al. 2015). On the other extreme, breeding onset in Arctic species depends on snow cover in spring and is restricted to a very narrow temporal window (Dickey et al. 2008).

The timing of breeding is a key determinant of breeding success and productivity (e.g. Verhulst 2008, Dunn and Moller 2014, Martin et al. 2014). In many woodland passerines, laying usually occurs so that the nestling period matches the seasonal peak in caterpillar abundance, which in turn is determined by weather conditions, such as temperatures in spring (Lof et al. 2012). Breeding too early or too late in relation to optimal conditions may lead to lower breeding performance (Robb et al. 2008). Seasonal declines in breeding outputs have been observed in many species, with birds breeding earlier in the season having higher reproductive outputs than those breeding later on (Verboven and Visser 1998, Mougeot and Bretagnolle 2006, Verhulst and Nilsson 2008). This pattern may arise when individuals breeding earlier in the season are of better quality, and/or when environmental conditions degrade as the season progresses (e.g. worsening weather conditions, reduced food abundance and quality, degrading breeding habitat vegetation; Verhulst et al. 1995, Verhulst and Nilsson 2008). The latter scenario implies that optimal conditions for breeding are temporally limited within a breeding season. In a context of climate change and rapidly changing environmental conditions, a preexisting synchrony between the timing of breeding and the availability of key breeding resources (seasonal food peak) may be disrupted leading to biodiversity loss (Visser et al. 2004), but more investigation is needed on this topic (e.g. Visser and Both 2005, Reed et al. 2013, Grimm et al. 2015).

Recent research has also indicated that seasonal declines in breeding performance may vary in strength depending on habitat type or location. For example, Zarybnick et al. (2015) found that Tengmalm's Owl (*Aegolius funereus*) showed different seasonal declines in productivity in temperate and boreal areas, principally due to differences in nestling mortality rates across the season. In the Great Tit *Parus major*, clutch size declines through the breeding season have been reported in rural, but not in urban areas (Wawrzyniak et al. 2015). This may imply that conditions for breeding in the latter habitat are more stable or last longer in the year, which may have implications for the ecology of these populations. However, with these few exceptions, the variability in declines of seasonal reproductive performance remains poorly studied or explored.

Research on the relationship between timing of breeding (i.e. lay date) and breeding output (e.g. clutch size, success or productivity) in birds, up until now, has been mainly conducted in temperate and boreal regions (Barnard et al. 1987, Amar et al. 2012, Dunn and Møller 2014). Relatively few studies exploring the association between timing of breeding and breeding outputs have been conducted in the Southern Hemisphere, particularly in Africa (Simmons 2000, Lepage and Lloyd 2004, Martin et al. 2014, Murgatroyd et al. 2016). Identifying these associations may contribute to our understanding of why some populations are more or less successful under certain circumstances and conditions than others. This may be particularly important when dealing with endangered species, as it may allow prioritizing conservation efforts of target species in space or time (Green et al. 2006, Amar et al. 2008, Gangoso et al. 2009).

The Black Harrier (*Circus maurus*) is a ground-nesting medium-sized bird of prey, endemic to southern Africa. The species is very scarce with an estimated total world population of less than 1000 mature breeding birds, a distribution range of approximately 500,000 km² and a far more restricted breeding range of approximately 170,000 km² (van der Merwe 1981, Siegfried 1992, Simmons 2000). This endemic species to Southern Africa is listed as endangered in both South Africa and Namibia (Taylor et al. 2015, Simmons et al. 2015), the two countries encompassing the totality of the breeding range. Black Harriers breed in both coastal regions and in the interior mountains of south-western South Africa (Curtis et al. 2004, Curtis 2005), but the species remains very understudied (Van der Merwe 1981, Simmons et al. 1998, Curtis et al. 2004, Curtis 2005, Simmons et al. 2005, Jenkins et al. 2013) and information on breeding parameters is particularly scarce. Curtis et al. (2004) explored variation in breeding parameters between nests in coastal or interior-mountain regions, finding that clutch sizes and productivity were greater in coastal regions. However, this study used data from only 3 years (2000–2002) and their analyses did not account for variations due to the timing of breeding or the influence of weather. Black Harriers are known to lay clutches over an extended period (from mid-May to mid-December, Simmons et al. 2005), but information about variation in the timing of breeding between years or regions is currently lacking. The breeding range of the Black Harrier mainly coincides with the Mediterranean climate zone of South Africa, characterized by cold and wet winters (May–September), and warm and dry summers (October–April). The seasonal fluctuations characterizing this climatic zone may in-

fluence the timing of breeding for Black Harriers, which may also differ between the main nesting regions.

In this study, we use a large data set of nearly 400 breeding events of this scarce endemic species collected over 15 years (2000–2014) in South Africa to investigate spatial-temporal variations in breeding performance. We first report on regional variation in the timing of breeding, and its association with weather conditions (i.e. rainfall and temperature). We then investigate whether key breeding parameters (clutch size, nesting success and productivity) vary depending on the timing of breeding, geographical location (coastal vs. interior-mountain regions) and weather conditions. Lastly we evaluate whether seasonal declines in breeding performance differ in strength between regions, and the potential implications this might have for the conservation of this species.

Material and methods

Study area

Breeding data were collected opportunistically over a large area (ca. 170,000 km²) of temperate southwestern South Africa (29°–34°S; 17°–27°E) from 2000 to 2011. More focused studies took place along the west coast of the Western Cape Province and inland in the Northern Cape Province around Nieuwoudtville (31°19'S; 19°05'E) first from 2000 to 2002, and then from 2012 to 2014. Nests were located in and around national parks (i.e. South African National Parks – SANParks), provincial protected reserves (i.e. Cape Nature), or on private lands. They were spread across a mosaic of different biomes with diverse habitats and vegetation types, many of which are nationally and internationally protected and considered of high biological and ecological values (see e.g. Manning 2007). Climate across the study area varies between provinces: the west of the Eastern Cape, and Western Cape have a more temperate climate and a winter rainfall regime (April to September), while the coastal Northern Cape also experiences a winter rainfall regime but with more fluctuating temperatures (South African Weather Services: <http://www.weathersa.co.za>).

Black Harriers are ground-nesting birds and, unlike other raptor species, breeders rarely re-use the same nest over the years (Simmons et al. 2005). It is as yet unclear if the same individuals breed together as a pair year after year, although some evidence suggests this is not the case (Garcia-Heras et al., unpublished data). Breeding sites were located by observing areas where Black Harriers were previously known to breed and/or where perched adults were detected. As in other raptor species, the females take care of the chicks at the nests and perform all brooding, while the male captures and provides the food in the early nestling period (Simmons 2000, Redpath et al. 2002a). Thus, nests were located by following prey-carrying males and observing where females landed after a food pass (Simmons 2000).

Breeding parameters

After discovery, nests were visited regularly (usually 2–3 times per breeding event) where possible to assess nesting success and productivity. However, because of the extensive nature of the study area, not all breeding areas and nest sites were monitored consistently each year, and for some remote areas, nests sites were only visited once, or were last visited prior to fledging. During each nest visit, we noted the nest contents (i.e. number of eggs or nestlings) and, if the nests contained nestlings, a visual estimate of age was taken. In a subsample of nests, wing, tail and tarsus length (mm), and mass (g) of chicks were measured. Nest visits were kept as brief as possible (< 20 min) and an effort was made to leave the vegetation around the nest undisturbed. The location of nests was recorded using a global positioning system (GPS). A total of 490 nests were located between 2000 and 2014, although not all variables examined in this study were available for each breeding attempt, so sample size varies among analyses.

Lay dates were estimated by subtracting 31 days (Simmons et al. 2005) from hatch date, which was in turn estimated either directly when a clutch was found with an egg hatching or a newly hatched chick (aged 1–3 days old) or indirectly from nestling age. Nestling age was estimated either visually (see above) or through body measurements (using data from a subsample of nests that were visited more regularly, we could build growth curves of wing-length for this species, Garcia-Heras et al. unpublished data). Given the variation in precision of lay dates among nests, we finally attributed the laying date for each nest to a 15-day period (where 1 = 1–15 May, 2 = 16–31 May, etc., up to 15 = 1–15 December). For the sake of simplicity, we henceforth refer to these lay date periods as “lay date” even though they are not exact dates. Lay date could not be determined for nests located during the incubation period and visited only once or that failed before the second visit ($n = 70$), or for nests discovered after fledging or for breeding records without a precise visit date ($n = 18$); therefore, data from these nests were excluded from the breeding phenology analyses. Overall, lay date was estimated for 402 breeding events.

Clutch size was defined as the maximum number of eggs laid. When possible, nests were visited twice during the incubation period with the second visit timed to coincide with the estimated date of hatch. This ensured that we recorded the exact number of eggs laid per breeding event. Nests that were visited before the clutch was finished and that subsequently failed, or only during the nestling period were excluded from clutch size analyses. Clutch size was known for 191 breeding attempts.

Breeding output was measured in two ways, nesting success (known for $n = 263$ breeding attempts) and productivity ($n = 261$). Nesting success was classified as 1 for those nests where at least one young was raised to 35 days old, or 0 otherwise. Productivity was defined as the number of young reaching 35 days of age (range 0–4) for pairs that laid a clutch. Black Harriers fledge at approximately 40 days old (Simmons et al. 2005) but in many cases our last visit occurred before that age; however, in harriers, as in many other species there is usually little mortality during this late nestling stage (Redpath et al. 2002a). Thus, we assume that any nestlings alive at 35 days old would have fledged.

Topographic parameters

Nest coordinates were incorporated in a geographical information system (QGIS Valmiera 2.2.0), projected on WGS84-UTM-34S as the coordinate reference system. Using this GIS, we calculated and identified the following variables for each nest: i) Altitude, from the Shuttle Radar Topography Mission (SRTM) 90 m Digital Elevation Database v4.1 (Srtm90m). ii) Region (coastal and interior-mountain) was defined using a combination of nest altitude (from SRTM) and distance to the coast. Coastal nests were defined as those located within 15 km from the coast and with a maximal altitude of 100 mASL ($n = 328$). Nests located further than 15 km from the coast and with an altitude higher than 100 mASL were considered as interior-mountain ($n = 146$). However, this classification excluded nine nests that were located higher than 100 mASL (average of 118 m), but within 15 km from the coast and for the purpose of our analysis these were classified as coastal. Another eight nests were located at an altitude lower than 100 m, but 45 km from the coast, and these were classified as interior-mountain. In both cases, we believe our classification to more accurately describe conditions for those 17 nests. This regional classification was initiated by Curtis et al. (2004) to explore regional differences in lay dates and productivity of Black Harriers. That study also further differentiated between nests in mountain and interior-lowland areas. However, overall sample size of interior-lowland areas was too small to allow meaningful comparisons, and so these two categories were grouped together as a single region (interior-mountain) for our study.

Weather data

Weather data were obtained for the period 2000–2014 from 17 weather stations distributed throughout the study area (source: South African Weather Services: <http://www.weathersa.co.za>) (Figure 1). For some stations, weather data were lacking in certain months or years (due to technical problems or stations not being active at the beginning of our study period). For each weather station, we obtained daily rainfall (mm) and daily maximum and minimum temperature (°C). From these, we calculated monthly averages for daily temperature and daily rainfall for all the weather stations and years when data were available. Each weather station was classified as “coastal” or “interior-mountain” depending on its location, using the same criteria as for nests. We attributed to each nest the weather data from the nearest weather station located within the same region. An exception was however made for 18 nests located in interior-mountain regions, but for which the corresponding closest weather station was located 230 km away: for these we instead used the closest coastal weather station, as the distance between these nests and this weather station was relatively small (i.e. between 35 and 70 km away), and because they had a similar altitude. On the other hand, we excluded weather data entirely for 6 nests for which the distance between them and their closest weather station was further away than 120 km. Overall, our sample size included 475 nesting events with associated weather data from weather stations that were located on average 29 ± 22 (SD) km away from study nests (Figure 1).

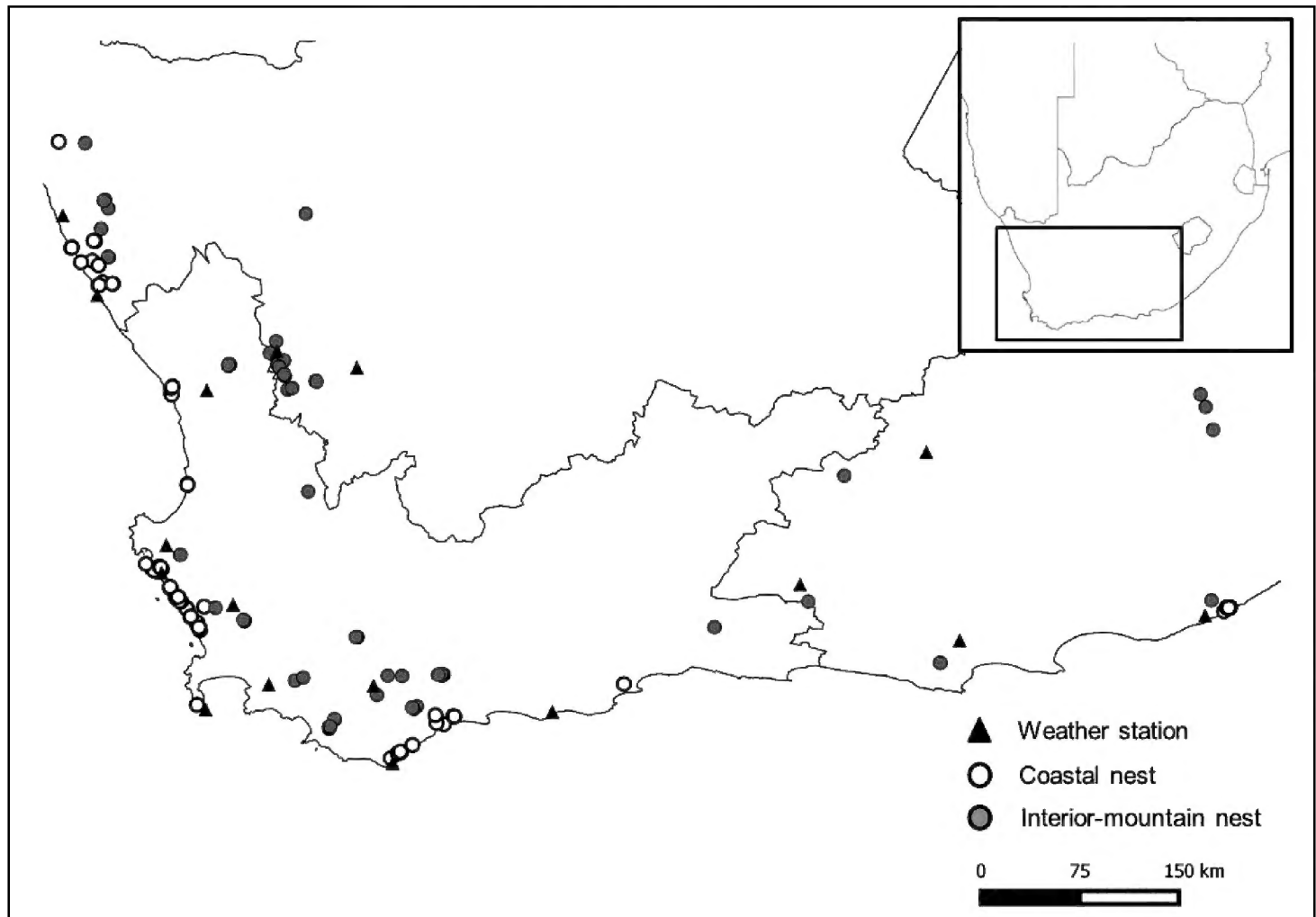


Figure 1. Location of study nests within South Africa for which weather data were available ($n = 475$), during 2000–2014. White circles: coastal nests; dark grey circles: interior-mountain nests; black triangles: weather stations that provided data for the purpose of the study.

Statistical analysis

All statistical analyses were conducted using R 3.2.3 (the R Foundation for statistical computing 2015).

To reduce the number of weather variables and to account for potential collinearity among them, we conducted a Principal Component Analysis (PCA) on monthly rainfall and temperature data for each station and study year. We selected the first four weather Principal Components (PCs) for subsequent analyses (a scree plot showed a marked drop in explained variance between the fourth and the fifth PC). PCs were chosen for analyses on the effect of weather on breeding parameters, rather than using raw weather data, because we did not have a strong *a priori* hypothesis of the time period over which weather may be more influential. Therefore, using raw data would have meant exploring the effect of a high number of potential explanatory variables (weather over different time periods). Furthermore, our PCs had clear biological meanings (see results), which helped in interpreting the relationships found. However, because PCs include information about weather in all months, in our discussion we placed most emphasis on the meaning of each PC for the months prior to the variable in question (e.g., for the relationship between lay date and weather, we focus on the meaning of each PC for the months prior to laying, not subsequently).

We investigated regional differences in the weather PCs using General Linear Mixed Models (GLMMs, statistical package lme4, Bates et al. 2012) that included the weather station identity as a random effect (to take into account the non-independence of the data coming from the same station) and the factors region (coastal vs. interior-mountain) and year (14 levels) as explanatory variables. This analysis was run on a data set that had only one data point for each weather station and year ($n = 88$).

To analyse factors affecting variation in breeding phenology, we used GLMMs that included year as a random effect, so that we could identify patterns that would describe what happens in an average year. The “lay date” of each nest (response variable) was fitted with a Gaussian distribution and an identity link function. The initial model included the explanatory variables of region and weather variables (the first four weather PCs). These models were conducted on a subsample of 393 nests for which both lay date and weather data were available.

GLMMs with year as a random effect were also used to explore clutch size, nesting success and productivity (response variables) in relation to region, lay date, and weather (explanatory variables). Initial models also included the interaction between region and lay date to look for regional differences in seasonal variations in breeding performance. For models where this interaction was significant, we re-ran the same model but without the interaction to test for differences between regions. Nesting success was fitted with a binomial distribution, and clutch size and productivity were fitted with a Gaussian distribution. Even though the latter may not be ideal for productivity data, using a Poisson distribution produced models with large dispersion parameters, whereas Gaussian models performed well and model residuals were normally distributed. Analyses of clutch size were conducted on a subsample of 183 breeding events for which clutch size, lay date and weather data were available. Analyses of variation in nesting success and productivity were conducted on a subsample of 223 and 222 breeding events, respectively, for which lay date and weather data were also available.

A stepwise backward procedure was performed for model selection (with the function drop1), and likelihood ratio χ^2 tests (LRT) on AIC differences were used to select the best models.

Samples sizes differed between regions and our slope estimates for the relationships between lay date and breeding parameters could be influenced by this or hinge on data from a few very early or very late nests (see Figure 3). In order to be confident that regional differences were not simply a consequence of these potential biases, we randomly selected a reduced and equal number of nests in each region and re-estimated the slope of the relationships and their 95% confidence intervals using a bootstrap analysis implemented in R 3.2.3. For the relationships between lay date and clutch size, our sample sizes included 144 and 42 nests in the coastal and interior-mountain regions, respectively, so we re-estimated the slope using 1000 random samplings of 30 nests from each region. For the relationships between lay date and productivity, our sample sizes included 163 and 64 nests in the coastal and interior-mountain regions, respectively, and we re-estimated the slope using 1000 random samplings of 50 nests from each region.

Results

Weather: seasonality and regional differences

Study regions were characterized by different weather conditions (Figure 2a, b). Both regions experienced higher temperatures and little rain during summer months (December-March) than winter months (May-September). However, temperature differences between summer and winter were more pronounced in interior-mountain than in coastal regions. Additionally, coefficients of variation for both temperature and rainfall were greater from April to October in the interior-mountain than in the coastal region, indicating that weather conditions in interior-mountain regions at that time were more variable in space (among nest localities) or time (years) than those in coastal regions. Rainfall levels strongly decreased (by half) between August and September in both regions, coinciding with the peak of lay date in Black Harriers (Figure 2b, c).

The PCA analysis on monthly rainfall and temperature data rendered four PCs explaining approximately 60% of the variance (Table 1). PC1 was positively related to temperature during all months, although the relationship was less marked during the winter months (June-August) when temperatures were overall lower (Figure 2a). PC2 was positively related to rainfall during all months, although the relationship was less marked during the summer and early autumn months (December-March), when rainfall levels were overall lower (Figure 2b). PC3 contrasted high temperatures in summer and early autumn (December-March) but low in late autumn and winter (May-August), with lower temperatures in summer and higher in autumn-winter. Therefore, this PC refers to temperature seasonality. Finally, PC4 identified situations with higher rainfall in summer and early autumn (December-March), but lower rainfall in late autumn and winter months (May-August), thus referring to rainfall seasonality.

All weather PCs varied significantly among years, but only PC1 and PC3 were significantly different between regions (Table 2). PC1 values were lower in the coastal region (LS means: -1.15 ± 0.70), indicating cooler temperatures (particularly in springs, summers and autumns) than in the interior-mountain (LS means: 0.93 ± 0.64). PC3 values were also lower in coastal than interior-mountain region (LS means: -1.43 ± 0.34 and 1.18 ± 0.31 , respectively), indicating that temperature variation throughout the year was more pronounced in interior-mountain regions.

Timing of breeding

Lay date ($n = 393$ nests) was remarkably well spread through the year, spanning 8 months, from mid-May to mid-December, and followed a unimodal distribution in each region (Shapiro normality test, $w = 0.98$, $p = <0.0001$, $n = 287$ for coastal region; $w = 0.95$, $p = 0.0009$, $n = 106$ for interior-mountain region) with a peak during mid-August to end of September (Figure 2c).

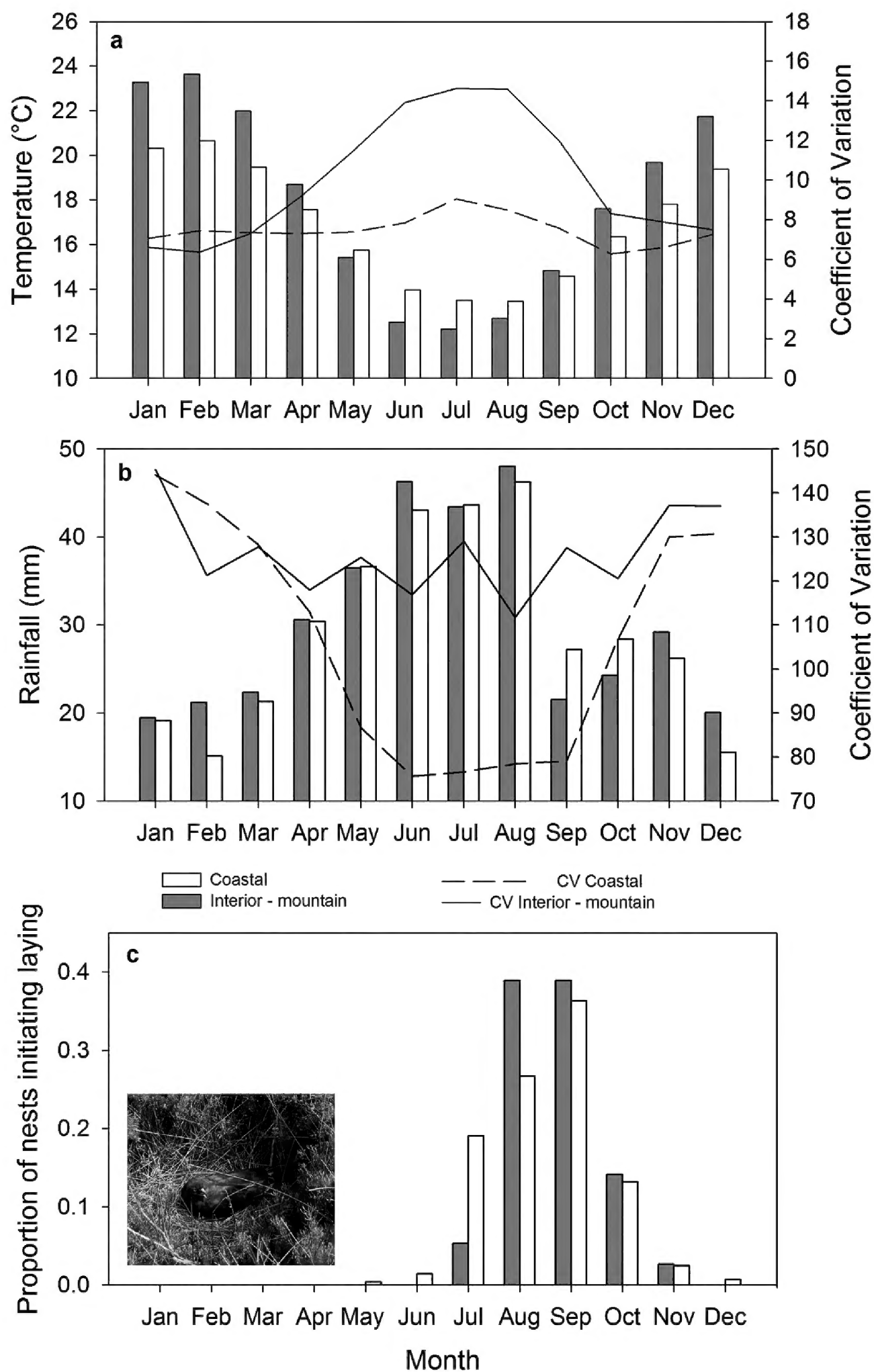


Figure 2. Monthly average temperature (a) and rainfall (b), according to region (coastal, white bars; interior-mountain, dark grey bars). Also presented are Coefficient of Variation (100x SD/Mean) for both climatic variables (dashed line for coastal, solid line for interior-mountain), as well as frequency distribution of breeding initiation ($n = 402$) (c) during the study period (2000–2014).

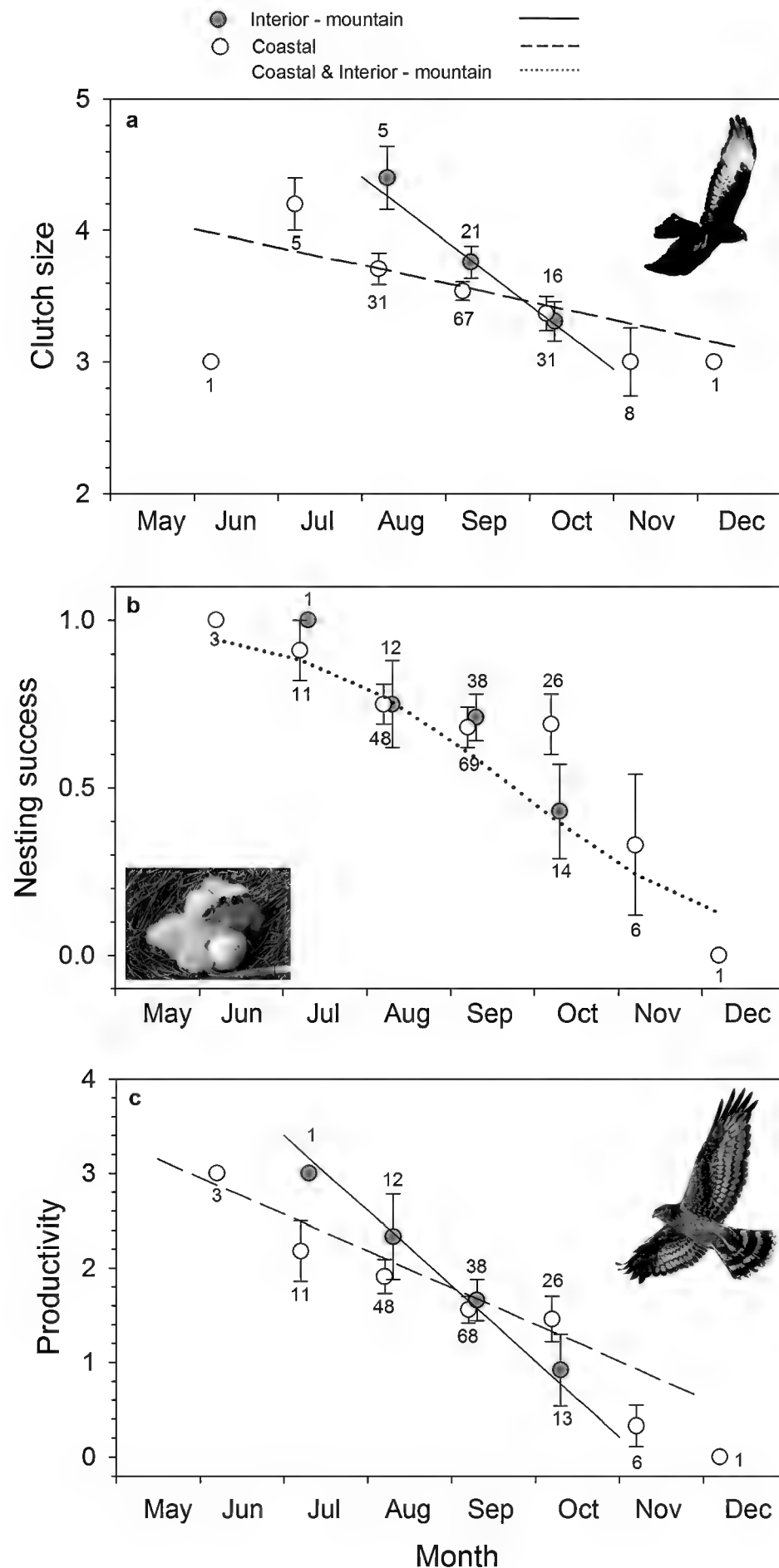


Figure 3. Black Harrier breeding performance (**a** clutch size **b** nesting success **c** productivity) variation according to lay date and region (coastal nests: white circles/dashed line; interior-mountain nests: grey dark circles/ solid line). Lines represent modelled data from the GLMM results (Table 3). Raw data (circles) are also shown for illustration purposes and have been averaged over two consecutive 15-days periods. Sample sizes (number of nests) are indicated above the error bars. The point line represents the breeding success variation with laying date for both coastal and interior-mountain regions (this relationship did not differ between regions).

Table 1. Results of the Principal Component Analysis conducted on weather data (monthly averages of daily rainfall and daily temperatures) collected in 2000–2014 at 17 weather stations (see Figure 1). “Temp” represents the average of the daily maximum and minimum temperatures (°C), per month. “Rain” corresponds to the average of the daily rainfall (mm) per month. Variable loadings greater than 0.2 or lower than -0.2 are highlighted in bold. The months during which Black Harriers usually breed are highlighted in grey.

	PC1	PC2	PC3	PC4
Rain. JAN	0.014443	0.129292	-0.01123	0.353204
Rain. FEB	-0.02877	0.171029	0.098396	0.416038
Rain. MAR	-0.01663	0.196125	0.032239	0.45707
Rain. APR	-0.06009	0.303045	0.03444	0.067087
Rain. MAY	-0.11894	0.281114	0.093557	-0.23835
Rain. JUN	-0.12415	0.308008	0.131795	-0.26365
Rain. JUL	-0.124	0.302469	0.084539	-0.23318
Rain. AUG	-0.13295	0.325751	0.102831	-0.27611
Rain. SEP	-0.09693	0.350088	-0.01698	-0.04674
Rain. OCT	-0.0634	0.28149	0.001479	0.105491
Rain. NOV	-0.07844	0.32201	0.029495	0.174901
Rain. DEC	0.006074	0.168862	0.060451	0.290475
Temp. JAN	0.292895	0.057873	0.310684	0.011043
Temp. FEB	0.315231	0.065366	0.257761	-0.01914
Temp. MAR	0.303027	0.066636	0.231843	-0.11742
Temp. APR	0.335735	0.082603	-0.02066	-0.20133
Temp. MAY	0.230807	0.16073	-0.29901	-0.07898
Temp. JUN	0.127701	0.149213	-0.44499	-0.0962
Temp. JUL	0.127055	0.120859	-0.43149	-0.10167
Temp. AUG	0.190731	0.153715	-0.36607	0.128207
Temp. SEP	0.272202	0.082607	-0.18223	0.075789
Temp. OCT	0.352615	0.052975	0.017441	0.024666
Temp. NOV	0.344244	0.035273	0.119129	-0.00367
Temp. DEC	0.290036	0.046253	0.258563	0.009631
Variance explained				
Proportion	0.254	0.1554	0.1361	0.08704
Cumulative	0.254	0.4084	0.5454	0.63249

Lay date was negatively associated with weather PC2 (slope = -0.26 ± 0.07) and PC4 (slope = -0.27 ± 0.10 ; Table 3), indicating that laying occurred relatively earlier under rainier conditions, particularly when rain was more intense in autumn, winter and spring, and when summers preceding laying were wetter. Lay date was also significantly different between regions (Table 3): nests located in coastal regions had overall earlier lay dates (LS means: 8.40 ± 0.22 , 15–30 August) than those located in mountain regions (LS means: 9.36 ± 0.28 , 1–15 September). Individuals in coastal regions also laid over a more extended period, with breeding events in this region occurring up to two months earlier and one month later than in the interior-mountain regions (Figure 2c).

Table 2. Results of the General Linear Mixed Models (GLMMs) testing for differences between years and regions (coastal vs. interior-mountain) in weather variables (PC1, PC2, PC3, and PC4; see Table 1). The “weather station” identity was included as a random effect to take into account for the non-independence of data from the same locality. DF: Degree of Freedom, LRT: Likelihood Ratio Tests.

Dependent variables	Explanatory variables	DF	LRT	P
PC1	Year	15	82.15	<0.0001
	Region	1	4.67	0.031
PC2	Year	15	32.11	0.006
	Region	1	0.02	0.88
PC3	Year	15	214.52	<0.0001
	Region	1	21.11	<0.0001
PC4	Year	15	95.19	<0.0001
	Region	1	0.04	0.83

Table 3. Results of the Generalized Linear Mixed Models (GLMMs) testing for variations in lay date (15-day periods), clutch size, nesting success and productivity. “Year” was included as a random effect in all models. Initial models included region (coastal vs. interior-mountain), weather variables (PCs) and lay date (for clutch size, nesting success and productivity), as well as interactions between region and lay date. Stepwise backward model selection was performed based on AIC values. We present the results of final models.

Dependent variables	Explanatory variables	DF	LRT	P
Lay date	PC2	1	15.00	0.0001
	PC4	1	7.28	0.007
	Region	1	16.14	<0.0001
Clutch size	PC2	1	4.23	0.039
	Region×Lay date	1	7.45	0.006
Nesting success	Lay Date	1	17.59	<0.0001
Productivity	PC2	1	5.08	0.024
	Region×Lay Date	1	2.84	0.092

Breeding parameters

Clutch size averaged 3.58 ± 0.64 eggs (range: 2–5; n = 183 nests). Clutch size varied with rainfall (PC2, Table 3), with larger clutches being associated with rainier conditions (slope = 0.08 ± 0.04), particularly in autumn, winter and spring. Clutch size also

varied significantly with the interaction between lay date and region (Table 3): clutch size declined markedly as the season progressed, but this decline was more pronounced in the interior-mountain (slope: -0.25 ± 0.07) than in the coastal region (-0.05 ± 0.03) (Figure 3a). Bootstrapping analyses using 1000 random samplings of 30 nests from each region indicated very little overlap between the estimates of slopes for each region (95% confidence intervals of -0.17 to 0.05 for coastal nests and of -0.39 to -0.15 for interior mountain nests). When removing the interaction region \times lay date from the model, clutch sizes were not significantly different between regions (LRT = 0.37, $P = 0.54$).

In total, 31% of nests ($n = 223$) monitored during the study period failed to produce fledglings. Nesting success declined significantly with lay date (Table 3; slope: -0.40 ± 0.10), and this decline was similar between regions (non-significant region \times lay date interaction; Figure 3b). Once controlling for lay date, no significant differences in nesting success were found between regions, nor any relationships between nesting success and weather variables (Table 3).

Productivity among monitored nests averaged 1.66 ± 1.30 fledglings (range 0 - 4 fledglings, $n = 222$ nests). Productivity was positively associated with weather PC2 (Table 3; slope = 0.12 ± 0.05), indicating that productivity increased in rainier conditions. Productivity also declined as lay date increased (Table 3; Figure 3c). As for clutch size, there was an indication that this seasonal decline in productivity differed between study regions (marginally significant region \times lay date interaction; Table 3; $P = 0.09$), with a steeper decline in the interior-mountain region (slope = -0.40 ± 0.12) than in the coastal region (slope = -0.20 ± 0.05 ; Figure 3c). Bootstrapping analyses using 1000 random samplings of 50 nests from each region showed that there was some overlap between the estimates of the calculated slopes for each region (Mean, SD, and 95% confidence intervals: -0.20 ± 0.05 , -0.30 to -0.08 for coastal nests; and -0.35 ± 0.14 , -0.59 to -0.12 for interior-mountain nests). When removing the interaction region \times lay date from the model, there was no significant difference in productivity between regions (LRT = 0.002, $P = 0.98$).

Discussion

This study revealed an extended breeding period for the Black Harrier and profound consequences of the timing of breeding on breeding performance. Moreover, it is one of the few studies that document a seasonal decline in breeding performance in a southern African species (Simmons 2000, Martin et al. 2014, Murgatroyd et al. 2016) and one of the few studies overall to highlight a regional difference in the strength of this seasonal decline. Seasonal declines in breeding performance appeared more pronounced in interior-mountain regions, characterized by more seasonally variable weather conditions, than in coastal regions. These observations may explain why coastal regions are seemingly more used by this scarce endemic species and have conservation implications, which we develop below.

Seasonal declines in breeding performance

Most strikingly, we found that seasonal declines varied among regions for clutch size and also (less markedly) for productivity. The seasonal decline in these parameters was progressive and moderate in coastal regions but much more abrupt in interior-mountain regions. Thus, clutch size and productivity were overall higher in interior-mountain than in coastal regions early in the season (until September), but differences were not found or values were higher in coastal regions for nests initiated from October onwards (Figure 3ac). Interestingly, we did not find a significant difference between regions for nesting success, suggesting that regional differences in declines in productivity may simply result from differences in clutch size patterns. Additionally, this suggests that differences between regions are more influential early in the breeding cycle. Ultimately, neither clutch size nor productivity were, on average, significantly different between regions, indicating that differences between regions early and late in the season balanced each other out.

Seasonal declines in breeding performance can be explained by differences in the quality of individuals breeding early or late and/or by a worsening of environmental conditions as the breeding season progresses (Verhulst et al. 1995, Verhulst and Nilsson 2008). The overall seasonal decline observed in the Black Harrier population may reflect a difference in the quality of individuals breeding earlier vs. later in the season (with e.g. older and more experienced birds breeding earlier in the season). However, the observed regional differences in the seasonal declines are unlikely to be explained by differences in individual quality alone, particularly for a mobile species like the Black Harrier (evidence from satellite tagged birds indicate that the same individual can breed in both the coastal and the interior-mountain regions in different years, Garcia-Heras et al., unpublished data). Our results thus indicate that changes in environmental conditions likely play an important role in explaining seasonal changes in breeding performance, and furthermore that this degradation in environmental condition is stronger in interior-mountain than in coastal regions.

Temperature was overall higher in coastal regions until August, when clutch sizes were smaller there, but the opposite pattern was found from October onwards, when clutch sizes were greater in coastal regions. Temperature variation could thus be an indicator of the temporal variation in quality of environmental conditions among regions. However, temperature (PC1) did not significantly influence clutch size (or any other breeding performance parameter), so differences are likely to be related to other factors, such as food availability or habitat quality. Black Harriers mostly feed on small mammals (ca. 65% of the diet), particularly on Four-Striped Mouse (*Rhabdomys pumilio*) and African Vlei Rats (*Otomys* sp.) (Jenkins et al. 2013, Garcia-Heras et al. unpublished data), so the smaller clutch size in interior-mountain areas for pairs starting to lay late in the season may reflect lower small mammal availability there at that time. Population dynamics and breeding output of the striped mouse are known to vary strongly with rainfall (see Taylor and Green 1976, Meynard et al. 2012, Rymer et

al. 2013). This, together with our results (relationship between PC2 and both clutch size and productivity), suggests that greater rainfall during autumn and winter could positively influence the abundance of small mammals such as Four-Striped Mouse, which may in turn influence breeding performance in Black Harriers, as found for other species (Korpimäki 1992, Salamolard et al. 2000, Redpath et al. 2002b). Future studies should investigate the relationship between Black Harrier's breeding and food availability, and how this varies in space and time.

Factors affecting lay date variations

Black Harriers showed a remarkably extended breeding period, with the onset of laying spread over 8 months (mid-May to mid-December). A wide spread in timing of breeding has been reported in other raptors from the Southern Hemisphere [e.g., 8 months for the Black Sparrowhawk (*Accipiter melanoleucus*), Martin et al. 2014], including other harrier species, such as the African Marsh Harrier *Circus ranivorus* (9 months, Simmons 2000, Simmons et al. 2005), the Cinereous Harrier (*Circus cinereus*) (7 months, del Hoyo et al. 1994) or the Spotted Harrier (*Circus assimilis*) (5 months, del Hoyo et al. 1994). This contrasts to what is usually observed in harrier species breeding in the Palearctic, for which the timing of breeding rarely exceeds 3 months [e.g., Pallid Harrier (*Circus macrourus*), Montagu's Harrier (*Circus pygargus*), Hen/Northern Harrier (*Circus cyaneus/hudsonius*), (Schipper 1979, Simmons et al. 1986, Arroyo et al. 1998, Simmons 2000, Amar et al. 2005, Terraube et al. 2009)]. These large scale differences in the extent of the timing of breeding are likely related to climate, the Northern Hemisphere being in general characterized by a more pronounced seasonality in rainfall and temperature regimes (Garcia and Arroyo 2001, Redpath et al. 2002a) than the Southern Hemisphere, limiting in time the conditions that are suitable for successful breeding, and also suggest that conditions for breeding are suitable over a longer time for Black Harriers, as for other African raptors.

Nevertheless, we found a clear seasonal peak, with most laying (ca. 50% of clutches) occurring between mid-August and the end of September. This, together with the strong seasonal decline in breeding performance observed, indicates that optimal timing for breeding is limited for this species, despite the overall large extended breeding period. This peak coincides with a sharp drop in rainfall levels and an increase in temperature (Figure 2), suggesting that high rainfall levels may impair laying. However, models showed that, overall, laying occurred earlier under more rainy conditions (negative relationships with PC2 and PC4), and particularly if rainfall was greater in autumn-spring periods and when summers preceding laying were wetter. The latter may reflect the east-west rainfall conditions in South Africa, as laying is earlier in eastern locations, where rainfall levels are overall higher particularly in winter months. This may also be associated with food availability: wetter summers may contribute to a greater primary productivity and subsequent rains just before (April-May) and during the time of breeding may lead to greater food abundance during Black Harrier's whole breeding cycle (see above).

The strong associations between timing of breeding, temperature and rainfall also indicate that climate change may further influence shifts in breeding phenology of southern African birds (Simmons et al. 2004, Cunningham et al. 2013), including raptors (Martin et al. 2014), most notably in the southern and western regions where a warming trend has been detected during the past 50 years, and rainfall is predicted to decline (Hockey et al. 2011, Cunningham et al. 2015). Our results highlight that weather conditions, and most notably rainfall regime, play an important role in determining the timing of breeding of Black Harriers, and likely shapes the regional differences encountered in lay date. However, the timing of breeding may also depend on the seasonal fluctuation of other variables responsive to environmental cues that change with weather conditions, but that were not tested here. These more likely would be either variations in food supply (Perrins 1970, Verhulst 2008) or arrival dates from the non-breeding grounds, as suggested for other raptor species (Newton 1998, Ketterson et al. 2015).

We also found differences in lay date between regions: Black Harriers breeding in coastal regions started laying on average about 15 days earlier, and clutches occurred over a more extended period than those breeding in interior-mountain (Figure 2c). These patterns suggest that optimal conditions for breeding might be achieved at different times in different geographical zones, but also indicate that suitable conditions for breeding may last longer in coastal than in interior-mountain regions.

Conservation implications

Black Harriers have been described as Fynbos specialists (Curtis et al. 2004), due to a greater number of breeding events in this vegetation type along the coast and a higher productivity in coastal regions compared with interior-mountain regions. However, our results, based on a larger sample size over a longer study period, differ from those of that study: while the number of monitored breeding events was indeed larger along the coast, we found that overall productivity was equal in interior-mountain and coastal regions. This was mainly explained by the regional differences in seasonal decline observed in breeding parameters, with clutch size and productivity being greater in interior-mountain regions early in the season, but the subsequent decline being more abrupt. Environmental conditions in interior-mountain regions might be more suitable than in coastal regions, but only for a limited period of about 1.5 months. Before, they seem to be unsuitable to allow breeding, and afterwards, they quickly deteriorate inducing a reduced breeding performance later in the season. Weather conditions at the beginning of the harrier breeding season (until October) also appeared much more variable among sites and years in interior-mountain regions (greater coefficient of variation; Figure 2ab). This implies that, even if average conditions are better at that time, in certain years or regions, conditions may not be suitable for breeding. In coastal regions, environmental conditions remain more stable throughout the harrier breeding season, which allows productive breeding to occur over a longer period of time (4 months). Thus, the more

stable weather in coastal regions within and among years may mean that it is overall a safer choice for Black Harriers to breed there than in interior-mountain regions. This may explain why breeding Black Harriers were more commonly found at the coast (i.e. 3 times more breeding events along the coast than in interior-mountain regions; Curtis et al. 2004), although we recognise that these figures do not control for search effort.

Recent changes in climate conditions within Africa during the last decades (Hockey et al. 2011, Kruger and Sekele 2012, Cunningham et al. 2015) may exacerbate the differences among regions and present a challenge for species like the Black Harrier. Indeed, a shift in rainfall and temperature patterns has occurred in South Africa and most notably in the south-west of the country, where most harriers breed: temperatures are getting warmer with less rain falling inland (the same pattern is expected in the western part of the Northern Cape Province, where many “interior-mountain” Black Harrier nests occur), while the opposite trend is expected along the coast (Cunningham et al. 2015). In addition, anthropogenic modifications in land use during the last century in South Africa such as the conversion of the Fynbos vegetation into agriculture or urbanization, might also negatively affect the Black Harrier population (Curtis et al. 2004). Only two records have mentioned Black Harriers breeding in cultivated areas (Steyn 1982, Chadwick 1997), which suggests that the species might not be capable of adapting to breed in non-natural habitats (Curtis et al. 2004, Jenkins et al. 2013), contrary to Palearctic harriers (Arroyo et al. 2002, Millon et al. 2002) and other south African raptors (Murgatroyd et al. 2016). Further land use change may “force” even more Black Harriers to breed along the coast, in Fynbos vegetation, where environmental conditions remain more stable within and among years in comparison to other available sites (e.g., Karoo biome in interior-mountain regions) that may become drier and colder. This highlights the importance that the coastal Fynbos may have for the stability and sustainability of the Black Harrier population in the future. Conservation measures have already prioritized the protection of Fynbos vegetation, through the creation of national parks and private reserves, and should continue in order to conserve the species in the long term.

Conclusions

This study provides unique evidence for spatial variation in the strength of seasonal declines in breeding performance. This main finding has broad implications for population biology and conservation. Environmental heterogeneity needs to be accounted for when considering overall population viability, and our findings suggest that where environmental conditions are less variable and more predictable, the timing of breeding may have less importance for the production of young. Relative differences in individual quality between early and late breeders, which can explain the breeding seasonal declines (Verhulst and Nilsson 2008) would also potentially matter less. These areas may therefore constitute population sources and play a key role for overall population viability. In areas where seasonal declines are more pronounced, a mistiming of breed-

ing will reduce offspring production and populations will be less buffered from rapid, unpredictable environmental changes. Studying spatial variations in the strength of seasonal productivity declines, as we did with the scarce and endemic Black Harrier, could help identify important breeding areas for long-term population viability.

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